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BIOSYSTEMATICS OF PSILOSTROPHE DC. (COMPOSITAE) I. CHROMOSOME VARIABILITY[1]

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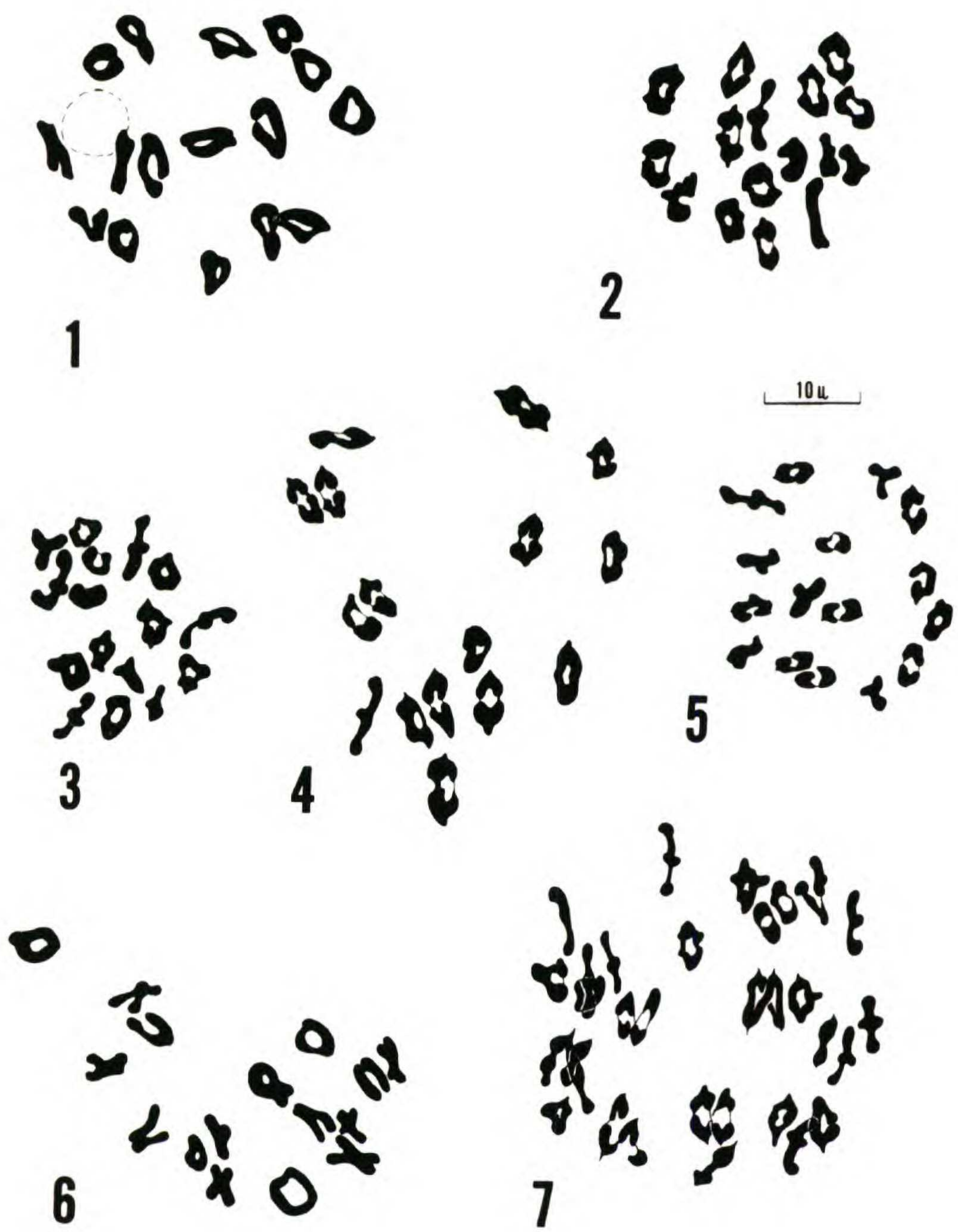
The genus *Psilostrophe* DC. (Compositae:Helenieae) consists of seven species of conspicuous, weedy herbs commonly referred to as paperflowers, which are common and showy elements of the summer flora in the semiarid regions of the southwestern United States and adjacent Mexico. The species are closely related and most taxonomic difficulties apparent in the genus arise from the substantial morphologicai similarities of the species. It was conceivable that a study of chromosome numbers and meiotic behavior in wild plants and studies of experimentally synthesized hybrids might help to clarify the evolutionary relationships and status of the taxa. The purpose of this paper is to summarize information on chromosome numbers in the genus and present evidence of structural hybridity and numerical variation in some species.

MATERIALS AND METHODS

Meiosis was studied in cells undergoing microsporogenesis. For this purpose young capitula collected in the field or greenhouse were fixed in a modified Carnoy's solution of chloroform: 95% ethanol: glacial acetic acid (4:3:1 V/V/V) and placed under refrigeration as quickly as possible. After a period of 24 to 48

[1]I thank Donald J. Pinkava for his guidance in this study, which formed part of a thesis submitted in partial fulfillment of the requirements of the Ph.D. degree at Arizona State University, Tempe. I also gratefully acknowledge Harlan Lewis for his review of this paper.



Figures 1–7. **Camera lucida drawings of meiotic chromosomes of Psilostrophe.** 1, *P. bakeri*, diakinesis, $2n = 16_{II}$ (*Brown 754–5*); 2, *P. cooperi*, metaphase I, $2n = 16_{II}$ (*Brown 385–8*); 3, *P. gnaphalodes*, metaphase I, $2n = 16_{II}$ (*Brown 813–2*); 4, *P. sparsiflora*, metaphase I, $2n = 16_{II}$ (*Brown 542*); 5, *P. tagetina*, metaphase I, $2n = 16_{II}$ (*Brown 617–1*); 6, *P. villosa*, diakinesis, $2n = 16_{II}$ (*Higgins s. n.*); 7, *P. mexicana*, metaphase I, $2n = 22_{II} + 5_{IV}$ (*Brown 788–3*).

hours, the fixed material was transferred to 70% ethanol and stored under refrigeration. Entire florets were stained in aceto-carmine. The stained anthers were teased free from the floret and squashed in a drop of Hoyer's solution yielding a semi-permanent preparation (Beeks, 1955). Mitotic metaphase chromosomes were studied in root tip cells. Following a pretreatment in 1% colchicine for four hours, root tips were similarly fixed and stored. After softening in a solution of HCl: 95% ethanol (1:1 V/V) for three minutes, the root tips were stained with aceto-carmine and squashed in Hoyer's solution. Voucher specimens are deposited in the Arizona State University Herbarium (ASU); duplicates to be distributed.

RESULTS

The base chromosome number (x) in *Psilostrophe* is 16 (Tables 1 & 3). Observations of somatic chromosomes show a symmetrical karyotype of uniform chromosomes all of a similar length and possessing a median to submedian centromere (Figure 8). The diploid species investigated possess one pair of satellite chromosomes; otherwise, individual chromosomes could not be distinguished.

The counts reported in Table 1 indicate that polyploidy is rare in the genus, manifest only in the tetraploid, *Psilostrophe mexicana,* but chromosome variability within populations is common in several diploid species. These chromosomal differences occur as both structural rearrangements and as differences in the presence and number of supernumerary (B) chromosomes.

Structural hybridity. The principal chromosome rearrangements detected were reciprocal translocations which were found in naturally occurring populations of five of the six diploid species (Table 3 & Figures 9–14). Plants heterozygous for one or occasionally two reciprocal translocations are recognizable by the formation of one or two rings of four chromosomes in metaphase I. Plants which have such ring configurations occasionally exhibit a chain of four chromosomes due probably to the failure of chiasmata formation in one arm (Figures 12 & 13). Only *Psilostrophe sparsiflora* of the diploid species is found thus far to be free from translocation heterozygosity, and it is limited in distribution to a relatively small geographical region in southern

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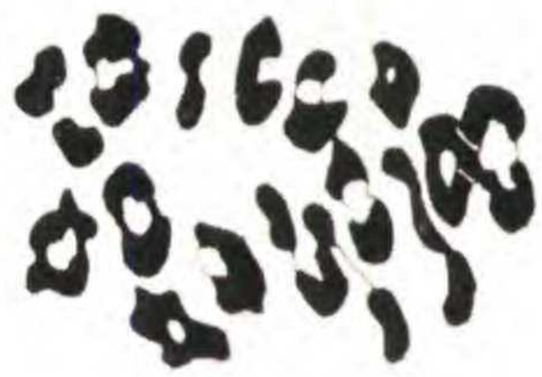

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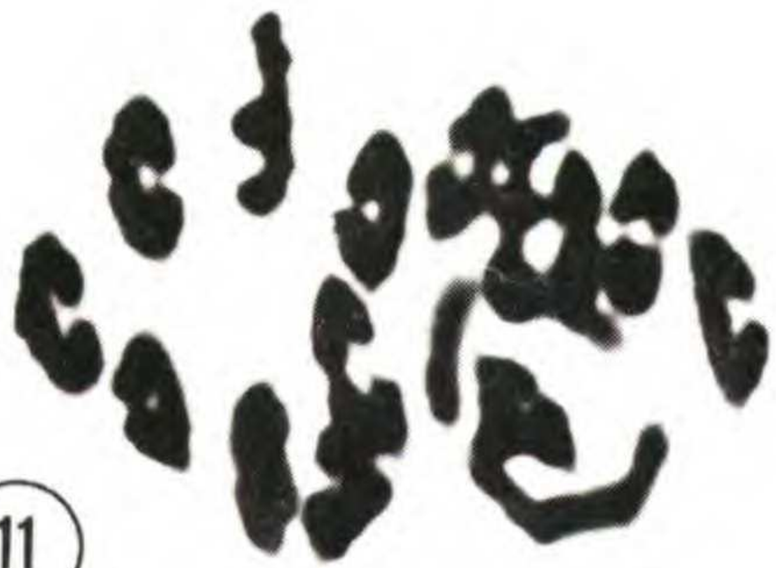

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Utah and northern Arizona where it does not appear to be actively evolving as evidenced by the uniform morphology of different populations. However, only a few populations have been examined cytogenetically and additional study may well establish the presence of translocation heterozygosity in this species. As may be seen in Table 3, over a third of the populations studied in each of the five remaining diploid species contained at least one plant heterozygous for a single translocation. Although numerous multivalent configurations were observed in the tetraploid *P. mexicana,* they are not considered here because of the inherent difficulties in distinguishing tetravalents due to duplications of chromosomes from tetravalents due to translocation heterozygosity.

Only a relatively few individuals from each population were examined cytogenetically in this initial survey. Thus, while plants heterozygous for one or more translocations are known to be geographically widespread, very little is known of the frequency of translocation heterozygosity within populations, although the frequency with which they have been found suggests it is quite high. Two distinct populations of *Psilostrophe tagetina* from the foothills of the Chiricahua Mountains in southeastern Arizona were examined in greater detail than the rest. Of the twelve plants examined from a population located near Paradise on the eastern slopes of the Chiricahuas, three (25%) were found to be heterozygous for a single translocation. The other population examined is located in the western foothills near the historical site of Fort Bowie. Eight plants from this population were examined cytologically; six (75%) were heterozygous for one or more translocations. Two interchanges occurred in one plant which consistently possessed a meiotic configuration of $12_{II}+2_{IV}+1B_{I}$

Figure 8. **Mitotic chromosomes of Psilostrophe tagetina.** $2n = 32 + 1B$ (arrow); cell from squash of colchicine treated root tip. × 1200.

Figures 9–14. **Translocation heterozygosity in species of Psilostrophe.** All × 1200. 9, *P. bakeri,* photomicrograph, metaphase I, $2n = 14_{II}+1_{IV}$ (*Brown 764*); 10, *P. cooperi,* camera lucida drawing, metaphase I, $2n = 12_{II}+2_{IV}$ (*Brown 622-1*); 11, *P. gnaphalodes,* photomicrograph, metaphase I, $2n = 14_{II}+1_{IV}$ (*Keil 7895*); 12, *P. tagetina,* photomicrograph, metaphase I, $2n = 12_{II}+2_{IV}$ (rings) + $1B_{I}$ (*Brown 399*); 13, same as 12 but with one ring quadrivalent and one chain quadrivalent; 14, *P. villosa,* camera lucida drawing, metaphase I $2n = 14_{II}+1_{IV}$ (*Higgins s. n.*).

Table 1. **Meiotic Configurations in Natural Populations of Psilostrophe.**

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe bakeri (A. Gray) Greene	**United States:** COLORADO: Delta Co.: 14.2 mi NW of Delta along Hwy 50, *Brown 759-2 & 759-3.*	$16_{II}(2)$*
	United States: COLORADO: Delta Co.: Tongue Creek Orchards NW of Orchard City, *Brown 764.*	$14_{II}+1_{IV}(1)$
	United States: COLORADO: Mesa Co.: W of Grand Junction, *Brown 754-1 & 754-5.*	$16_{II}(2)$
Psilostrophe cooperi (A. Gray) Greene	**United States:** ARIZONA: Graham Co.: Cemetery ridge overlooking Solomon, *Brown 401-2.*	$16_{II}(1)$
	United States: ARIZONA: Maricopa Co.: 14 mi S of Aquila along Eagle Eye Road, *Lehto 3578.*	$16_{II}(1)$
	United States: ARIZONA: Maricopa Co.: Cave Creek, *Brown 385-8.*	$16_{II}(1)$
	United States: ARIZONA: Mohave Co.: .25 mi E of Burro Creek, *McLeod 453 & 452.*	$16_{II}(1)$; $14_{II}+1_{IV}(1)$
	United States: ARIZONA: Pima Co.: Organ Pipe National Monument, *Pinkava 10035.*	$14_{II}+1_{IV}(1)$
	United States: ARIZONA Pima Co.: 4.1 mi SSW of Redington along road to Tanque Verde, *Pinkava 10942 & 10941.*	$16_{II}(1)$; $14_{II}+1_{IV}(1)$
	United States: ARIZONA: Santa Cruz Co.: N of Elgin along Hwy 83, *Brown 622-1.*	$12_{II}+2_{IV}(1)$
	United States: ARIZONA: Yuma Co.: 13 mi N of Wenden. *Pinkava 10354.*	$16_{II}(1)$

Table 1 (Continued).

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe gnaphalodes DC.	**Mexico:** COAHUILA: 11.3 mi S of Rio Salada along Hwy 57, *Keil 7874B.*	$16_{II}(1)$
	Mexico: COAHUILA: ca. 63 mi S of Monclova along Hwy 57, *Pinkava 10529 & 10530.*	$16_{II}(2)$
	Mexico: COAHUILA: 50 mi S of Piedras Negras; 1.6 mi N of El Infante along Hwy 57, *Keil 7840.*	$14_{II}+1_{IV}(1)$
	Mexico: COAHUILA: 23 mi W of Paila along Hwy 40, *Keil 7965*[a]	$16_{II}(1)$; $14_{II}+1_{IV}(1)$
	Mexico: COAHUILA: 5.3 mi E of Paila along Hwy 40, *Keil 7955 & 7955*[a].	$16_{II}(1)$; $12_{II}+2_{IV}(1)$
	Mexico: COAHUILA: 1.5–6.5 mi E of General Cepeda along Hwy 40, *Brown 813-2 & 814-1.*	$16_{II}(1)$; $12_{II}+2_{IV}(1)$
	Mexico: COAHUILA: Muralla Pass 46.2 mi S of Monclova, *Keil 7895.*	$14_{II}+1_{IV}(1)$
	Mexico: NUEVO LEON: 6.7 mi E of San Roberto along road to Linares, *Pinkava 10550.*	$16_{II}(1)$
	United States: TEXAS: Brewster Co.: 1.2 mi N of Persimmon Gap Ranger Station, *Keil 7830.*	$14_{II}+1_{IV}(1)$
Psilostrophe mexicana R. C. Brown	**Mexico:** CHIHUAHUA: 7–8 mi N of junction to Jiménez along Hwy 45, *Brown 788-1, 788-3 & 789-1.*	$18_{II}+7_{IV}(1)$; $22_{II}+5_{IV}(2)$
	Mexico: CHIHUAHUA: Between Parral and Jiménez 2.6 mi W of Hwy 49, *Keil 8238.*	$22_{II}+5_{IV}(1)$
	Mexico: DURANGO: La Resolana, *Brown 800.*	$24_{II}+4_{IV}(1)$
	Mexico: DURANGO: 2.7 mi S of La Zarca along Hwy 45, *Brown 803-1 & 803-4.*	$22_{II}+5_{IV}(1)$; $14_{II}+9_{IV}(1)$

Table 1 (Continued)

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe sparsiflora (A. Gray) A. Nels.	**United States:** ARIZONA: Coconino Co.: Meteor Crater, *Brown 493 & 536.*	$16_{II}(2)$
	United States: ARIZONA: Coconino Co.: 5 mi NW of Wupatki Natl. Monument, *Brown 542.*	$16_{II}(1)$
	United States: ARIZONA: Coconino Co.: N of Sunset Crater at Natl. Forest boundary, *Brown 420.*	$16_{II}(1)$
	United States: ARIZONA: Mohave Co.: 2 mi W of Peach Springs on Hwy 66 then .4 mi N along Buck and Doe Road, *McLeod 1011.*	$16_{II}(1)$
Psilostrophe tagetina (Nutt.) Greene	**Mexico:** CHIHUAHUA: 8.7 mi W of Hwy 45 along Hwy 2, *Keil 8448 & 8448*[a].	$14_{II}+1_{IV}1B_{I}(2)$
	Mexico: CHIHUAHUA: 8.4 mi S of Nuevo Casas Grandes, *Keil 8396.*	$16_{II}(1)$
	United States: ARIZONA: Apache Co.: 1.2 mi E of Hwys 180 and 666 along Hwy 60, *Brown 617-1 & 617-2.*	$16_{II}(1)$; $16_{II}+3B_{I}(1)$
	United States: ARIZONA: Cochise Co.: Chiricahua Mtns.; junction of Portal Road and road to Paradise, *Brown 819-1.*	$16_{II}(1)$
	United States: ARIZONA: Cochise Co.: Paradise, *Brown 398, 821-1-11.*	$16_{II}(2)$; $14_{II}+1_{IV}(1)$; $14_{II}+1_{IV}+1B_{I}(1)$; $16_{II}+1B_{I}(3)$; $16_{II}+1B_{II}(1)$; $16_{II}+2B_{II}(1)$
	United States: ARIZONA: Cochise Co.: 5.3 mi S of Fort Bowie turnoff along Hwy 186, *Brown 399, 601, 604-608.*	$16_{II}(3)$; $14_{II}+1_{IV}(4)$; $12_{II}+2_{IV}+1B_{I}(1)$
	United States: ARIZONA: Cochise Co.: Apache Pass, W of the summit, *Brown 825-2 & 825-3.*	$16_{II}+1B_{I}(1)$; $12_{II}+2_{IV}(1)$

Table 1 (Continued)

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe tagetina (Nutt.) Greene (Continued)	**United States:** NEW MEXICO: Grant Co.: .3 mi S of Hwy 61 along Hwy 180, *Keil 8461A*.	$16_{II}+1B_{I}(1)$
	United States: NEW MEXICO: Santa Fe Co.: 7.3 mi N of Stanley along Hwy 41, *Keil 7648*.	$16_{II}(1)$
	United States: NEW MEXICO: Torrance Co.: 10 mi E of Mountainair, *Keil 7652*.	$16_{II}(1)$
	United States: TEXAS: Brewster Co.: Big Bend National Park: 15.1 mi N of Castolon, *Keil 7802A & 7802*[a].	$16_{II}(2)$
	United States: TEXAS: Brewster Co.: 13 mi E of entrance to Big Bend National Park, *Keil 7792*.	$14_{II}+1_{IV}(1)$
	United States: TEXAS: Jeff Davis Co.: Davis Mtns., *Keil 7701 & 7701*[a].	$16_{II}(1)$; $16_{II}+1B_{I}(1)$
Psilostrophe villosa Rydb.	**United States:** TEXAS: Randall Co.: ca. 1 mi NW of Canyon, *Higgins s. n. & s. n.*[a].	$16_{II}(1)$; $14_{II}+1_{IV}(1)$

*Number in parentheses denotes the number of plants examined.
[a]Cultivated from wild achenes.

(Figures 12 & 13), the maximum number of translocations detected in any one plant. One other plant from a nearby, but distinct, population also possessed two rings of four chromosomes but lacked the supernumerary chromosome.

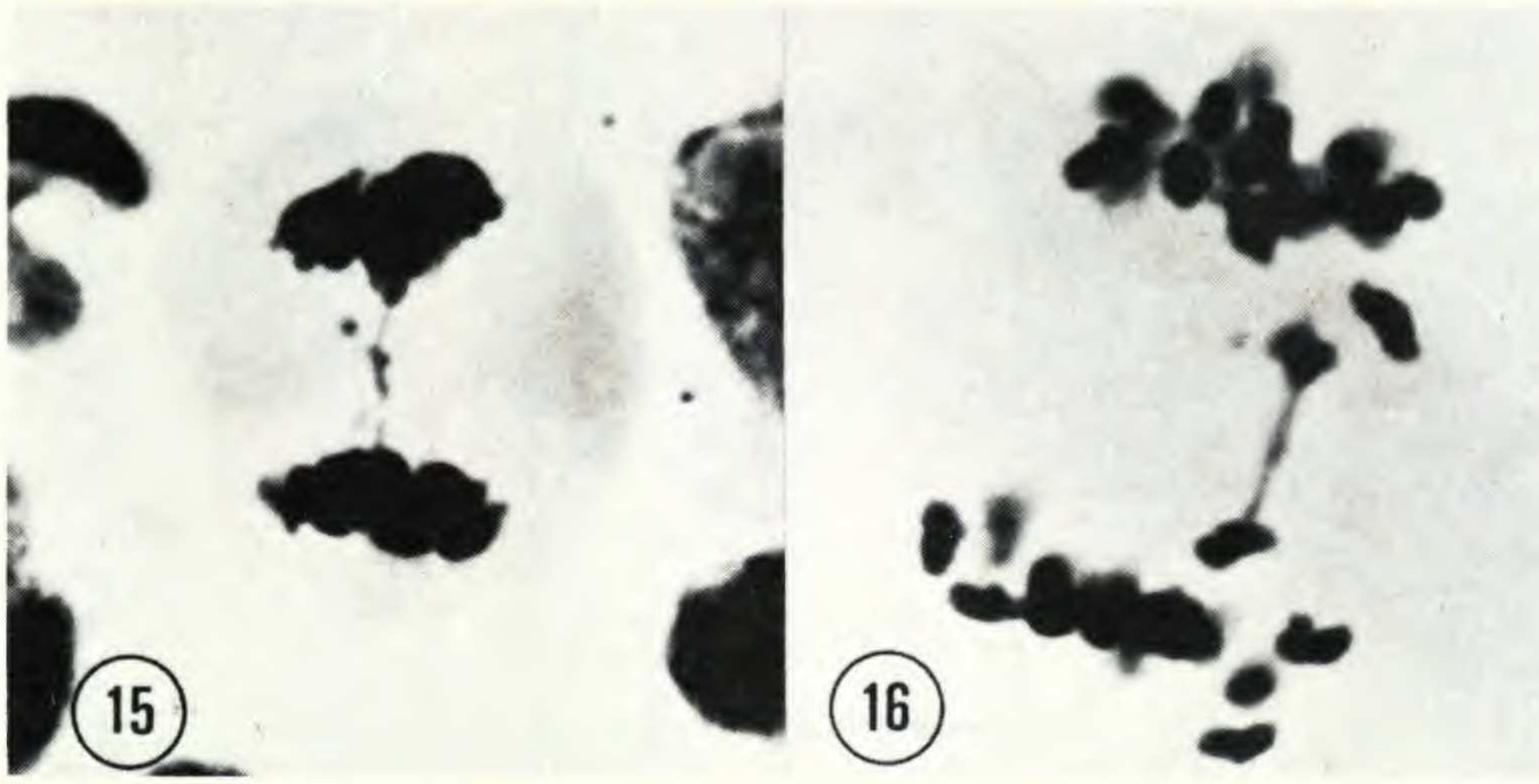
The ring of four configuration in *Psilostrophe* appears regularly to undergo an alternate segregation. Thus, the presence of interchange heterozygosity does not appear to lower the fertility appreciably. Pollen stainability in lactophenol-cotton blue (Maneval, 1936) is a high 92–99% in *P. tagetina* heterozygotes.

Plants heterozygous for inversions detectable by a bridge and fragment configuration are apparently much rarer than translocation heterozygotes in the genus, although "false-bridging" caused by stickiness of the chromosomes in anaphase I was particularly troublesome in this study. False bridges are fairly common in other genera of the Compositae and apparently do not adversely affect meiosis (Pinkava, 1964). Persistent anaphase I bridges plus an acentric fragment were observed in an individual of *Psilostrophe tagetina* (Figure 15) and one plant of *P. gnaphalodes* (Figure 16). Such inversions frequently occur in natural populations of flowering plants where they are, in most cases, only transitory and adaptively neutral unless they are associated with gene combinations of selective value (Stebbins, 1950). The role of inversion in the evolution of *Psilostrophe* is not known, but probably has had little effect for none of the artificial interspecific hybrids examined showed any evidence of inversion heterozygosity.

Chromosome configurations in experimental hybrids. Cytogenetic analysis of hybrids reveals a high degree of homology in chromosome structure among the species (Table 2 & Figures 17–23). In no case does the degree of heterozygosity for translocations in the hybrids exceed that present in the parental plants. The lack of evidence of meiotic abnormalities such as bridges, fragments or univalents makes it unlikely that the genomes of the species have been extensively rearranged.

Supernumerary chromosomes. From one to four supernumerary or B chromosomes frequently occur in natural populations of *Psilostrophe tagetina* (Table 3). While B chromosomes have not yet been detected in any of the remaining diploid species, their presence is to be expected in *P. gnaphalodes* and *P. villosa* for these two species are genetically closely related to *P. tagetina* (Brown, 1974b). An individual of *P. villosa* possessing 17 pairs of chromosomes has been reported (Powell & Turner, 1963) and 18 pairs plus 2 fragments has been reported in *P. tagetina* (Powell & Sikes, 1970). My study of *P. tagetina* suggests that these examples of extra bivalents probably represent paired supernumerary chromosomes.

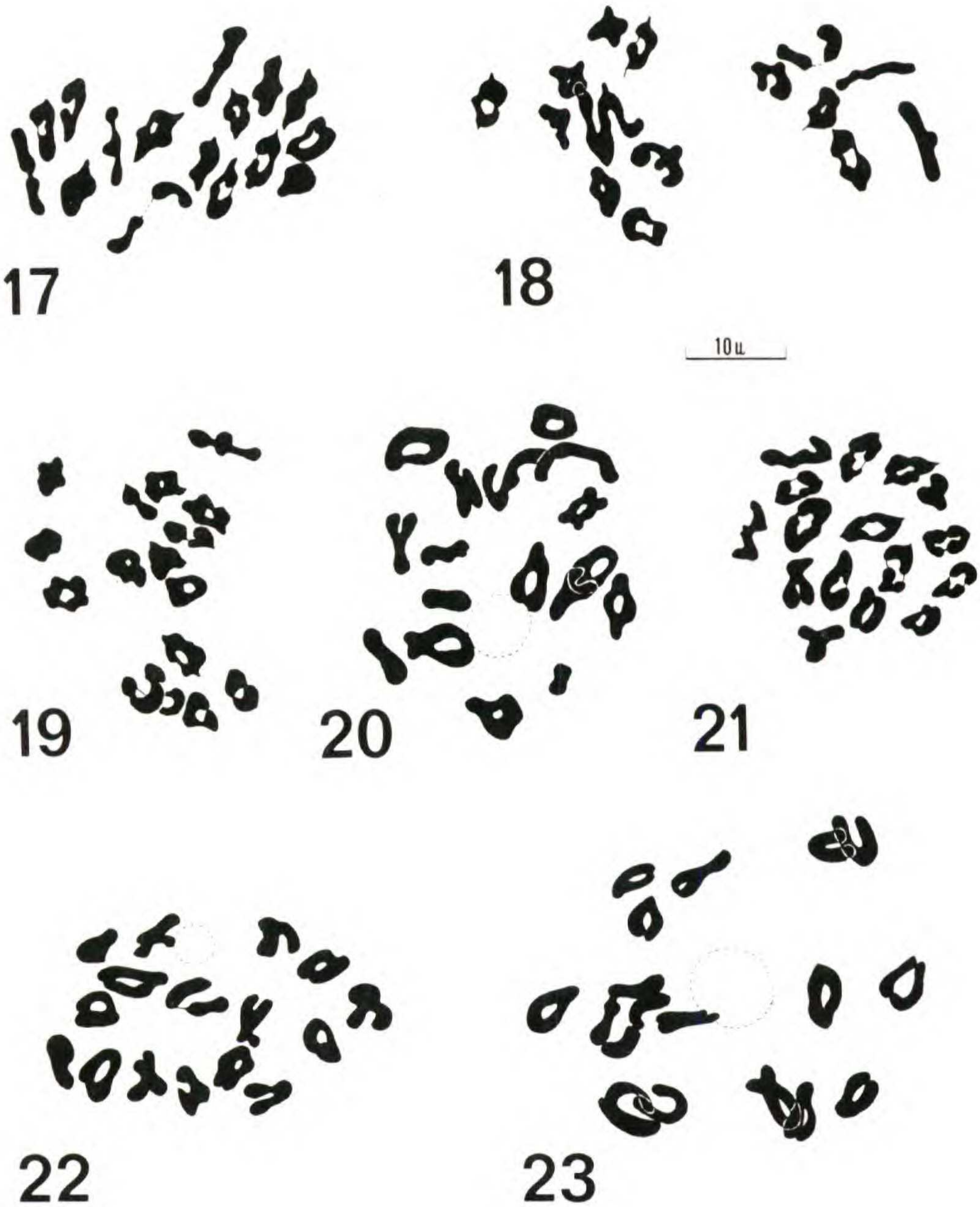
The occurrence of supernumerary chromosomes in *Psilostrophe tagetina* seems to be correlated with populations containing translocation heterozygotes as has also been reported in other



Figures 15 & 16. **Persistent anaphase I bridge and fragment configurations.** All × 1200. 15, *Psilostrophe tagetina* (*Keil 8461*); 16, *P. gnaphalodes* (*Keil 7955*).

groups of plants, e. g. *Clarkia* (Lewis, 1951 & 1968). Six of the twelve populations of *P. tagetina* examined contained individuals with B chromosomes and three of these populations also contain plants heterozygous for one or more translocations (Figure 24). I feel confident that when an adequate number of plants are sampled from additional populations an even stronger coincidence of B chromosomes and translocation heterozygosity will be found.

The supernumerary chromosomes apparently are stable in meiosis as indicated by the lack of chromosome lagging and subsequent micronucleus formation at the dyad or tetrad stages of meiosis. The occurrence of such micronuclei (Figure 25), although rare, does provide evidence of a mechanism for reducing the number of B chromosomes in the gametes. When only one supernumerary was present it could be detected as a univalent in prophase I through metaphase I (Figure 26). The supernumerary chromosomes showed no tendency to pair with any member of the regular complement. Anaphase I stages were rarely observed in *Psilostrophe tagetina;* the few that were adequate for analysis indicated that, in plants with one supernumerary, the supernumerary regularly undergoes a reductional division at anaphase I giving a 16–17 separation (Figure 27).



Figures 17–23. **Camera lucida drawings of meiotic chromosomes of experimental hybrids in Psilostrophe.** 17, *P. tagetina* × *P. gnaphalodes*, metaphase I, $2n = 16_{II}$; 18, *P. tagetina* × *P. villosa*, metaphase I, $2n = 14_{II}+1_{IV}$; 19, *P. sparsiflora* × *P. tagetina*, metaphase I, $2n = 14_{II}+1_{IV}$; 20, *P. sparsiflora* × *P. tagetina*, diakinesis, $2n = 16_{II}+1B_{I}$; 21, *P. sparsiflora* × *P. gnaphalodes*, metaphase I, $2n = 16_{II}$; 22, *P. cooperi* × *P. gnaphalodes*, diakinesis, $2n = 16_{II}$; 23, *P. cooperi* × *P. sparsiflora*, diakinesis, $2n = 14_{II}+1_{IV}$.

When two or more supernumerary chromosomes are present in a plant there is a marked tendency for them to pair in prophase I giving rise to bivalents which are decidedly smaller than the regular bivalents. An individual collected near Eager, Apache County, Arizona, was found to possess 16 regular bivalents plus 3 B chromosomes at metaphase I. In some microsporocytes the three supernumerary chromosomes formed a bivalent plus a univalent in prophase I (Figure 29); in others, the three supernumerary chromosomes occurred as univalents (Figure 28). No cases were observed in which the B chromosomes existed as a trivalent. Another plant from the eastern foothills of the Chiricahuas possessed 4 supernumerary chromosomes in addition to the A complement of 16 pairs. The majority of the microsporocytes examined in this plant showed the B chromosomes to exist as one pair and two univalents in prophase I. However, in some cells the supernumeraries occurred as two pairs of chromosomes which appeared to be joined by a single chiasma at diakinesis. The two supernumerary pairs are easily distinguished from the doughnut-like bivalents of the A complement by their smaller size and rod-like shape (Figure 30). The paired supernumerary chromosomes apparently separate regularly in anaphase I.

Polyploidy. The discovery of polyploidy in *Psilostrophe* has led to the recognition of a new species, *P. mexicana* (Brown, 1974a), with $2n = 64$. Tetraploidy was first noticed in the genus by De Jong and Longpre (1963) who reported an individual of *P. gnaphalodes* possessing 32 pairs of chromosomes. All subsequent counts show the tetraploids to possess from one to nine multivalents (Table 1), mostly as rings or chains of four chromosomes (Figure 7). Meiosis is regular for the most part although some lagging and persisting anaphase I bridges were observed. The evolutionary origin of this tetraploid taxon has not yet been studied experimentally. However, *P. mexicana* is morphologically and geographically most closely related to *P. gnaphalodes* and *P. tagetina* of the existing diploid species. I would point out that the existence of tetravalents in *P. mexicana* does not necessarily indicate origin by autotetraploidy, for the genomes of the aforementioned diploid species are closely related and artificial hybrids between them almost always show 16 bivalents in meiosis (Table 2 & Figure 17). Thus, the allopolyploid derivatives of such hybrids conceivably could possess several multivalents.

Table 2. **Chromosome Configurations in Experimental Hybrids of Psilostrophe.**

Cross & Meiotic Configurations[a]	Hybrid Configuration
INTRASPECIFIC CROSSES	
P. tagetina ($14_{II}+1_{IV}$) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	16_{II}
Reciprocal	$14_{II}+1_{IV}$
P. tagetina (16_{II}) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	$14_{II}+1_{IV}+1B_I$
INTERSPECIFIC CROSSES	
P. tagetina (16_{II}) × **P. gnaphalodes** ($14_{II}+1_{IV}$)	16_{II} (Figure 17)
Reciprocal	16_{II}
P. tagetina ($14_{II}+1_{IV}$) × **P. villosa** ($14_{II}+1_{IV}$)	$14_{II}+1_{IV}$ (Figure 18)
P. sparsiflora (16_{II}) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	$14_{II}+1_{IV}$ (Figure 19)
P. sparsiflora (16_{II}) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	$16_{II}+1B_I$ (Figure 20)
P. sparsiflora (16_{II}) × **P. gnaphalodes** (16_{II})	16_{II} (Figure 21)
P. cooperi ($14_{II}+1_{IV}$) × **P. gnaphalodes** ($14_{II}+1_{IV}$)	16_{II} (Figure 22)
P. cooperi (Undetermined) × **P. sparsiflora** (16_{II})	$14_{II}+1_{IV}$ (Figure 23)

[a]Ovulate parent listed first.

DISCUSSION

Individuals heterozygous for one or two reciprocal translocations frequently occur in populations of the diploid *Psilostrophe* species. The occasional occurrence of plants heterozygous for a translocation has been reported for a wide variety of flowering plants (for a review see Burnham, 1956). In the vast majority of cases the translocations are transitory and of minor evolutionary significance. It seems unlikely that the common and geographically widespread occurrence of translocation heterozygosity in the diploid species of *Psilostrophe* is due to chance alone. It is more probable that the chromosome structural hybridity is part of the adaptive genetic complex in these populations.

The high frequency of translocation heterozygosity found in *Psilostrophe* may have one of two explanations. The translocation heterozygotes may have an adaptive superiority to either of the two possible homozygous conditions, or the chromosomally polymorphic populations may be the result of recent hybridization between populations differing by a translocation. That the chromosomally polymorphic populations may be the result of

recent hybridization seems highly improbable. Translocation heterozygosity has been observed in five of the six diploid species and often in widely disjunct populations. Also important is the finding that interpopulational F_1 hybrids show no greater degree of translocation heterozygosity than intrapopulational experimental hybrids. It is reasonable to assume, therefore, that the widespread occurrence of translocation heterozygosity in the diploid species of *Psilostrophe* is due to the superior fitness of the heterozygotes themselves. However, as pointed out by John and Lewis (1966), while the theory of superior fitness of the heterozygote has often been put forth to explain systems of chromosome structure polymorphism, experimental proofs of the supposed heterozygous advantage are very few. An exceptional case for the existence of chromosome structure heterosis is found in *Drosophila* where certain polymorphisms (for inversions) are maintained chiefly by the superior fitness of the structural heterozygotes to either of the homozygous conditions when fitness is measured in terms of ability to metabolize nutrient media (Dobzhansky, 1961).

Translocation heterozygosity in *Campanula* has been demonstrated to function in maintaining genetic heterozygosity in the face of forced inbreeding by Darlington and LaCour (1950). In this example the greater the frequency of inbreeding, the greater was the selection for interchange heterozygotes. By analogy with this situation, translocation heterozygosity is believed to have similar effects in *Isotoma petraea* (Lobeliaceae) (James, 1965) and *Clarkia williamsonii* (Onagraceae) (Wedberg, Lewis, & Venkatesh, 1968).

In predominantly outbreeding plants such as *Psilostrophe*, translocations, like other structural rearrangements, may be important in restricting recombinational events. Translocations may allow the transmission of a favorable combination of genes as a block without the necessity of bringing the co-adapted genes together on the same chromosome (Stebbins, 1950). Of the three anaphase I disjunction patterns possible in a ring-of-four chromosomes, only the alternate pattern results in a balanced complement which is free from duplications or deficiencies, barring the very rare occurrence of cross-overs in the interstitial regions. In this manner recombination within a translocation is curtailed and a favorable linkage group maintained.

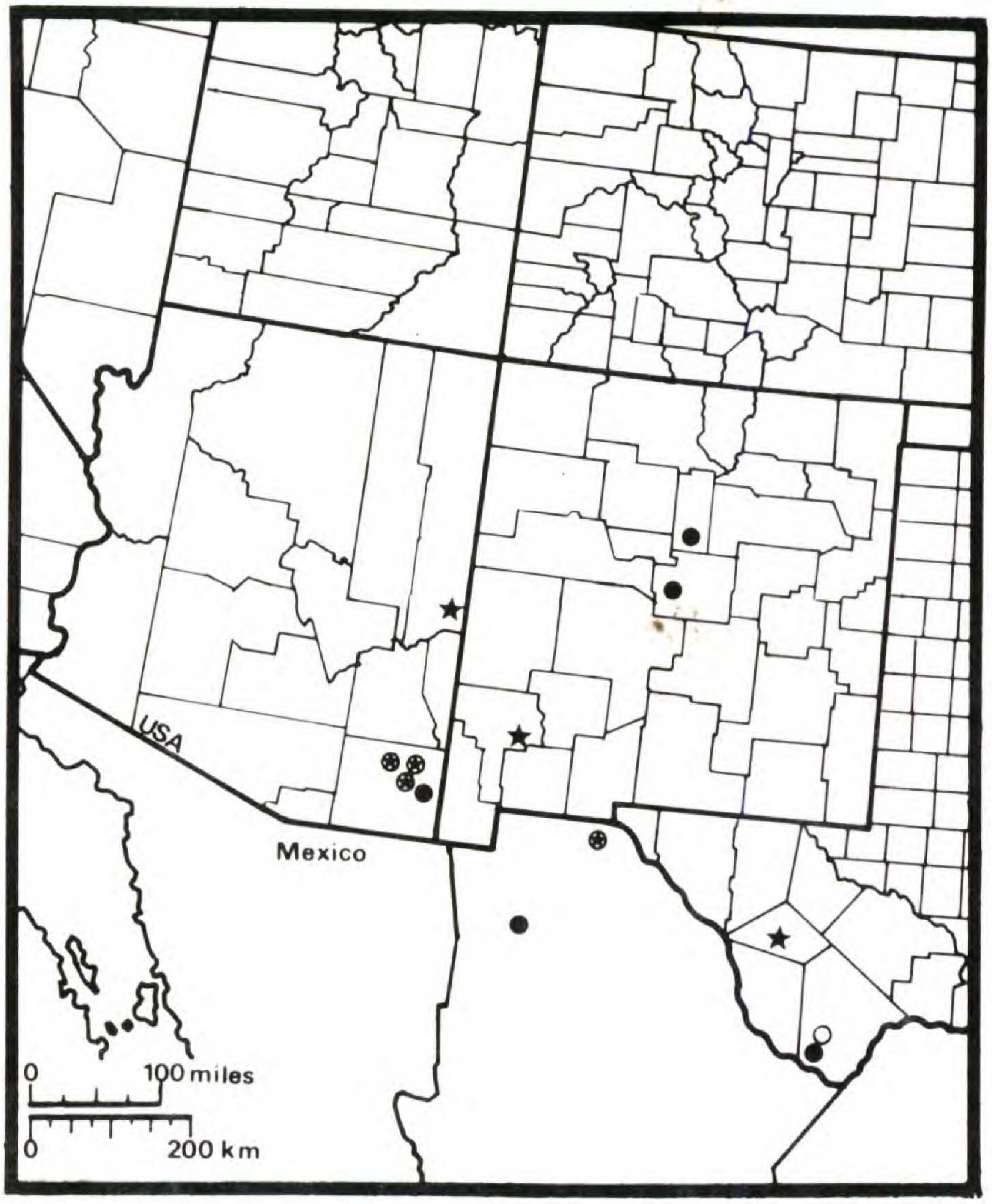
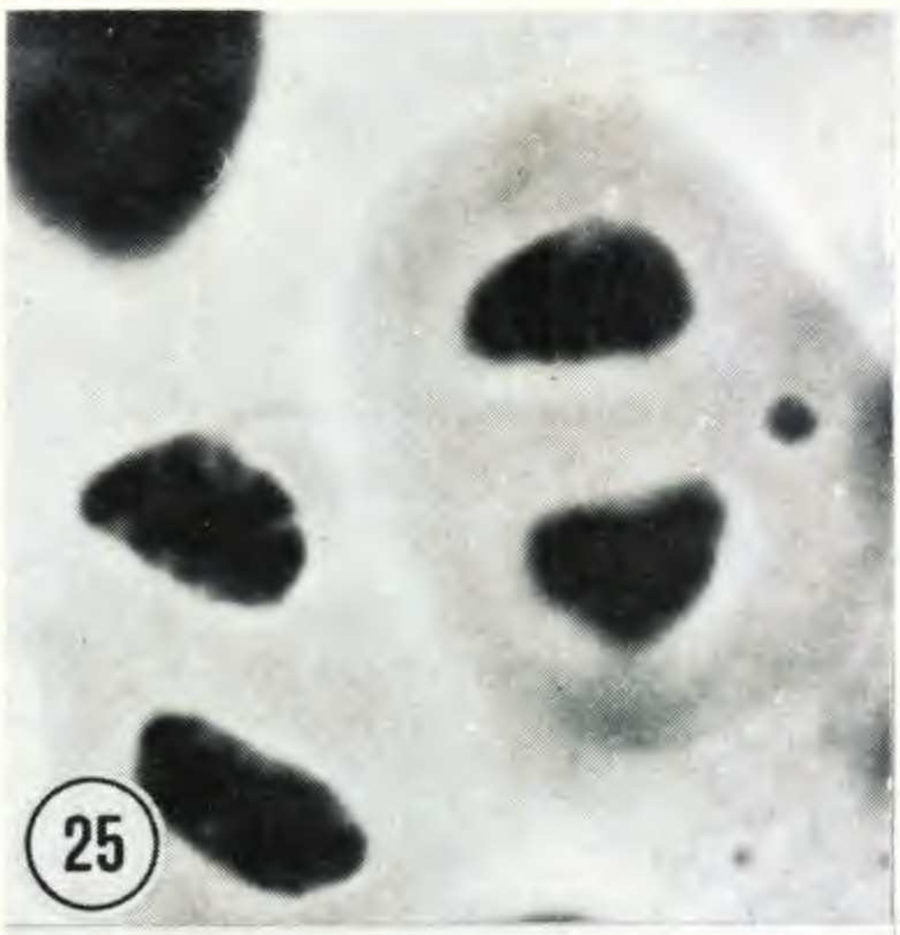
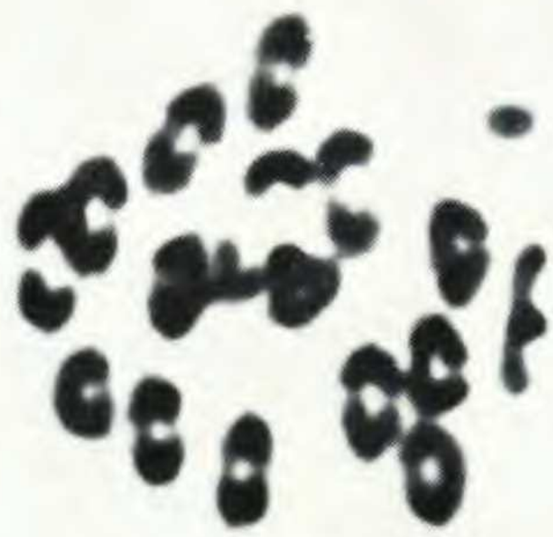
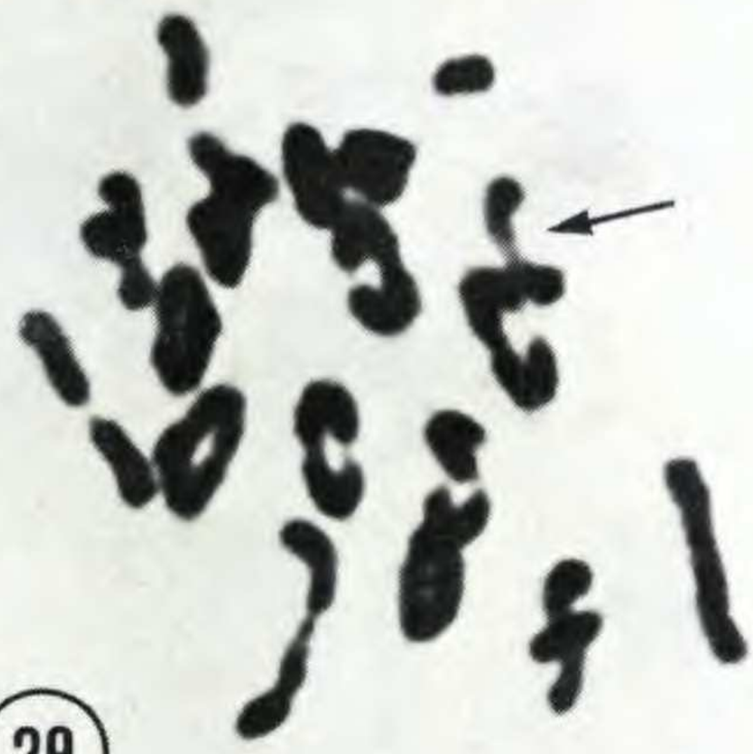


Figure 24. **Known distribution of supernumerary chromosomes and interchange heterozygotes in Psilostrophe tagetina.** Homozygous populations are represented by black dots; homozygous + B chromosomes are represented by black stars. Heterozygous populations are represented by white dots; heterozygous + B chromosomes are represented by circled stars.

Interchromosomal linkage can be realized only if interchange heterozygotes are not associated with a marked lowering of the fertility. The strong tendency of the ring-of-four chromosomes in *Psilostrophe* to undergo an alternate segregation in anaphase I results in the majority of the gametes with a balanced complement of genes. Thus, the presence of interchange heterozygosity in *Psilostrophe* does not result in a substantially lowered fertility when pollen stainability in lactophenol-cotton blue is used as an indicator of fertility. Such a non-random anaphase I disjunction pattern is known in other genera, e. g. *Oenothera* (Cleland, 1936)







Figures 25–30. **Meiotic behavior of supernumerary** (B) **chromosomes in Psilostrophe tagetina.** Figure 27 is a camera lucida drawing; all others are photomicrographs. Arrows indicate paired supernumerary chromosomes. All × 1200. 25, Dyad with micronucleus; 26, metaphase I, $2n = 16_{II}+1B_{I}$; 27, 16–17 segregation in anaphase I; 28, metaphase I, $2n = 16_{II}+3B_{I}$; 29, metaphase I, $2n = 16_{II}+1B_{II}+1B_{I}$; 30, diakinesis, $2n = 16_{II}+2B_{II}$.

and *Clarkia* (Lewis, 1953). Such plants are said to have a directed segregation (Burnham, 1956). According to Burnham, a directed segregation is dependent upon a karyotype with chromosomes of a uniform size with median to submedian centromeres. *Psilostrophe* is seen to possess such a karyotype, and in this respect, the structural hybridity is not unlike the well studied situations in *Paeonia* (Walters, 1942), *Clarkia* (Lewis, 1953), and *Oenothera* (Cleland, 1962). The development of a directed segregation also demands that chiasmata formation be confined to the ends of the chromosomes or terminalize very rapidly allowing sufficient flexibility for the ring to assume the "figure eight" configuration necessary in alternate segregation. Studies of chiasmata formation in *Psilostrophe* have not progressed sufficiently to say this is the case.

Interestingly, structural rearrangement of the chromosomes does not appear to have been a major force in the speciation of *Psilostrophe*. Analysis of interspecific hybrids failed to detect any individuals which possessed a greater degree of translocation heterozygosity than their respective parental taxa. Bivalents are the general rule in the experimental interspecific hybrids indicating that the genomes of the species have not been extensively rearranged. Often a translocation heterozygote of one species when crossed with a homozygote of another species yielded F_1 plants with 16 bivalents in meiosis. A similar situation is known in *Camissonia* (Onagraceae) in which hybrids between two subspecies show less evidence of structural rearrangement than do intrasubspecific hybrids (Moore & Raven, 1970). The role of structural rearrangement in the continuing differentiation of the various taxa is not known. Preliminary population studies suggest that isolated populations of *P. tagetina* may be undergoing cytological evolution and may differ from one another in the amount of translocation heterozygosity present. The amount and significance of cytological divergence among populations will be better understood when additional studies of interpopulational variation are carried out and when prime or standard types can be identified.

Although supernumerary chromosomes are now known to be common in flowering plants, having been reported in over 150 genera according to the estimate of W. V. Brown (1972), very little is known of their origin. It is likely that different types of B chro-

Table 3. **Chromosome Variability in Psilostrophe.**

Taxon	(*n*) Number	Individuals	Populations	*Translocation Heterozygosity* % Individuals	% Populations	*B Chromosomes* % Individuals	% Populations
P. bakeri	16	5	3	20	33	00	00
P. cooperi	16	10	8	40	50	00	00
P. gnaphalodes	16	13	9	46	67	00	00
P. mexicana	32	7	4	—	—	00	00
P. sparsiflora	16	5	4	00	00	00	00
P. tagetina	16	33	13	33	38	39	54
P. villosa	16	2	1	50	100	00	00

mosomes, or at least B chromosomes of different origins, occur. Misdivision and chromosomal fragmentation have been credited with giving rise to microchromosomes in *Oenothera* (Cleland, 1951) and *Caltha* (Reese, 1954). Certain supernumerary chromosomes in *Collinsia*, called "pseudosupernumerary" chromosomes by the authors, are thought to be derived from ordinary trisomics (Dhillon & Garber, 1960).

Better documented are the origins of B chromosomes in association with translocation heterozygosity in *Haplopappus* (Jackson, 1962) and *Clarkia* (Lewis, 1968; Lewis, Juhren & Mathew, 1971). In *Haplopappus* the supernumerary chromosomes apparently arise as nonessential centric fragments which persist after unequal reciprocal translocations. Whereas in *Clarkia*, B chromosomes arise from trisomics following non-disjunction in translocation heterozygotes. It is likely that in *Psilostrophe*, as in *Clarkia*, the B chromosomes arise initially from non-disjunction in translocation heterozygotes and originate, therefore, as partial trisomics. The correlation of supernumerary chromosomes with structural hybridity for translocations in *Psilostrophe tagetina* by no means proves that translocation heterozygosity was the factor contributing to the formation of B chromosomes in this taxon. It does seem, however, that carefully constructed breeding programs might add substantial evidence to reconstruct the origin of supernumerary chromosomes in this taxon.

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